Species turnover of aquatic organisms in space and time

Patterns in community composition and diversity

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Academic Dissertation

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ABSTRACT

The variation in biodiversity has intrigued ecologists for centuries. Currently, studying biodiversity is increasingly important because of its seminal role for maintaining ecosystem functions. Thus, one of the central questions in modern ecology is how species richness and composition can affect ecosystem functioning. Besides spatial variation in diversity, scientists are increasingly interested in the temporal patterns in diversity and community structure.

The aim of the PhD thesis was to study spatial and temporal turnover in aquatic communities. I investigated productivity-diversity relationships in three planktonic groups and at two spatial scales. Also, spatial patterns in community composition were compared among the three taxon groups and two spatial scales. Further, I studied the relationships between resource availability, species richness, biomass and resource ratio in phytoplankton communities. Temporal turnover in aquatic assemblages was studied in relation to several ecological, physical and geographical factors. Finally, within and between year variation in lotic diatom communities was investigated in Finnish streams showing wide variability in trophic status and size.

The results show that the relationships between ecosystem productivity and plankton diversity are highly variable, ranging from linear negative to linear positive and unimodal. Both alpha and beta diversity showed scale-dependency, highlighting that community patterns may be weaker at smaller scales covering shorter environmental gradients. I also found several key drivers affecting temporal variation in aquatic communities, such as study duration, latitude and organism body size. For example, turnover was faster in low latitude environments than at high latitudes at short time scales, but slower at long time scales. Ecosystem size seems also to be of high importance for turnover rate in many kinds of aquatic ecosystems.

This study revealed the suite of factors affecting aquatic species richness and composition both locally and regionally in several types of aquatic ecosystems. The results indicate how different types of communities and ecosystems change and are able to adapt to changing environmental conditions, such as increasing water temperatures or nutrient input due to global climate change. The factors affecting spatial and temporal components of diversity have an effect not only on the diversity and the identity of the biological organisms, but also on socio-economic well-being of humankind as we benefit from many resources and processes that are supplied by natural ecosystems, i.e. ecosystem services.

LIST OF ORIGINAL PUBLICATIONS AND CONTRIBUTION OF AUTHORS

This thesis is compiled from the results presented in the following publications. Each publication is referred in the text by its respective roman number.

I) Korhonen, J.J., Wang, J. & Soininen, J. 2011. **Productivity-diversity relationships in lake plankton communities**. PLoS ONE 6: e22041. The data collection and experimental design were done by J.J. Korhonen and J. Soininen. Structural Equation Modeling was conducted by J. Wang, Korhonen having the main responsibility of the analyses. The manuscript was written by J.J. Korhonen (corresponding author) and commented by J. Soininen.

II) Soininen, J. Korhonen, J.J., Karhu, J. & Vetterli, A. 2011. **Disentangling the spatial patterns in community composition of prokaryotic and eukaryotic lake plankton.** Limnology & Oceanography 56: 508-520. The data collection and experimental design were done by J.J. Korhonen and J. Soininen. Bacterial data analyses were conducted by J.J. Karhu and A. Vetterli. The rest of the analyses were done by J. Soininen. The manuscript was written by J. Soininen (corresponding author) and J.J. Korhonen.

III) Korhonen, J.J., Soininen, J. & Hillebrand, H. 2010. **A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems.** Ecology 91: 508–517. The data collection and experimental design were done by J.J.Korhonen and J. Soininen. J.J. Korhonen had the main responsibility of the analyses. The manuscript was written by J.J.Korhonen (corresponding author) and J. Soininen and commented by H. Hillebrand.

IV) Korhonen J.J., Köngäs P., Soininen J. 2013. **Variation in diatom assemblages in oligotrophic and eutrophic streams**. European Journal of Phycology 48: 141-151. The data collection and experimental design were done by P. Köngäs and J. Soininen. The data were analysed by P. Köngäs and J. Soininen. The manuscript was written by J.J.Korhonen (corresponding author) and commented by J. Soininen.

1. INTRODUCTION

1.2. Factors affecting communities in space

Biological communities comprise multiple interactive species each of which respond typically individually to underlying environmental or biotic drivers at multiple scales. In the next chapters, the influence of some of the key factors on spatial variability of community composition and richness are discussed in detail.

1.2.1. Productivity-diversity relationships

Due to the ongoing global decline in biodiversity, mainly caused by human activity, the number of studies examining factors affecting species richness has increased. In recent years, studies have especially focused on the causes of diversity patterns along specific gradients. One of the most central gradients associated with the variation in species diversity is **ecosystem productivity** (Waide et al. 1999). As productivity has a predominant role for species coexistence, the relationship between productivity and diversity (PDR) has become one of the main research areas in modern ecology. The relationship has direct applications for many central environmental issues, such as biodiversity conservation and ecosystem functions and services.

Species richness can be both a cause and a consequence of primary production, i.e. the rate of carbon fixed through photosynthesis. This dual role of biodiversity is based on two theories. First, the species-energy theory suggests that the amount of resource supply determines the number of coexisting species (Wright et al. 1983). Second, the studies in the field of biodiversity-ecosystem functioning (BEF) are built on the premise that species richness controls biomass production of a community. Combined with the resource ratio theory, these theories have also led to formulation of the multivariate hypothesis of PDR (Cardinale et al. 2009, Fig.1).

Even though the PDR has been widely examined using experimental approaches and observations, the underlying mechanisms still remain unclear. One of the most common mechanisms behind positive PDR is the *sampling effect*, which suggests that more diverse communities are more likely to comprise species that are notably effective in capturing resources and converting these into plant biomass (Loreau et al. 2001b). Studies spanning short temporal scales are especially prone to the sampling effect.

Another mechanism driving the PDR is *complementarity*, i.e. the differentiation of niches between the species present in a community (Loreau et al. 2001b). Niche differentiation is a process by which natural selection drives competing species into different patterns of resource use or different niches. As species' differences in using resources take time to have functional consequences in the ecosystems, niche complementarity is expected to affect productivity in the long-term only. Both sampling effect and complementarity may cause a positive linear PDR.

Unimodal PDRs are also typical in aquatic ecosystems (Waide et al. 1999).

In unimodal relationships, the number of species peaks at intermediate productivity. The low number of species at low and high ends of the productivity gradient can result from small amounts of resources and intense competition, respectively. Moreover, positive interspecific interactions (i.e., *facilitation*) can explain the coexistence of large numbers of species at the intermediate productivity.

Besides ecosystem productivity, the shape of the PDR is likely to be driven by the **spatial scale** of the study (Chase & Leibold 2002). In aquatic ecosystems, unimodal PDR are more common in studies which cover small (local) spatial scales, while positive linear relationships tend to dominate in studies covering larger (regional) scales. The increases of species dissimilarity with productivity within regions, i.e., more productive lakes or streams have more *multiple stable states* can be the main reason for the scale-dependency. The generality of the scale-dependency in PDR across organisms has, however, remained unresolved, as studies testing the scale-dependency are usually conducted in disparate systems using different study methods.

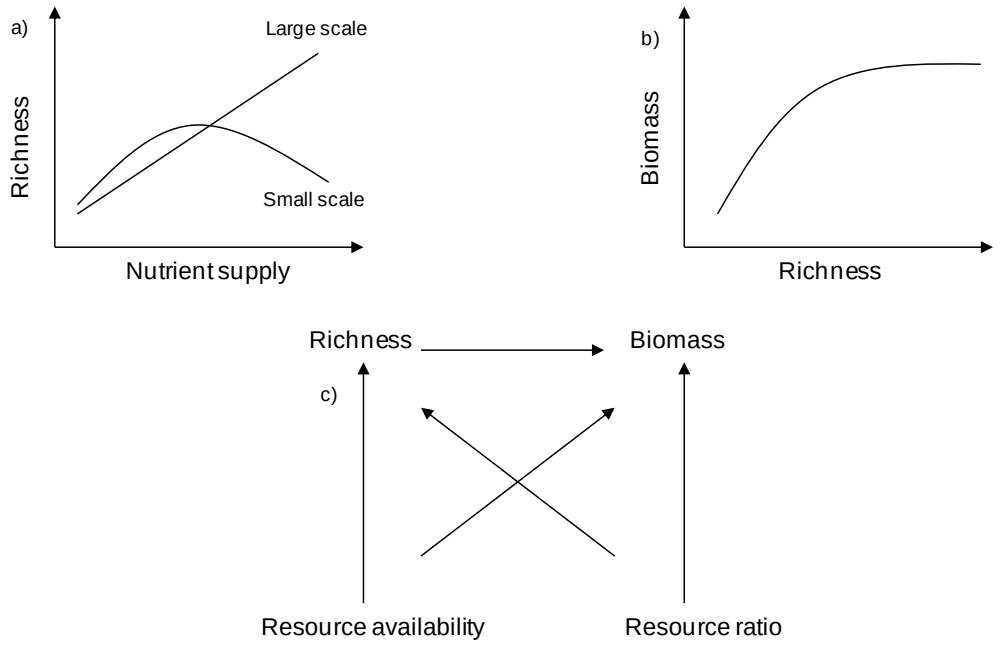

Figure 1.a) At small and large scale, the relationships between species richness and nutrient supply are predicted to be unimodal or linear, respectively. b) Biomass production first increases with species richness but saturates at high richness levels. c) The causal relationships between resource availability, species richness, biomass and resource ratio. (I)

1.2.2. Patterns in community composition

Biological communities are structured by the interaction between local and regional factors and processes (Ricklefs 1987; Leibold et al. 2004). Modern community ecology often examines metacommunities (sensu Leibold et al. 2004) which include multiple interacting metapopulations as well as studies the role of space in structuring communities in general. Metacommunities have wide practical implications for biodiversity conservation e.g. in fragmented landscapes.

The extent to which adjacent communities interact resulting in community homogenization (i.e. low beta diversity) is affected by species dispersal ability, which is, in turn, often related to species traits such as body size and dispersal mode. In recent decades, macroecological patterns have mainly been examined for larger organisms such as birds, fish and mammals (Blackburn and Gaston 2003). However, the study of microbial community structure has been focused on local environmental forcing instead of large-scale factors because microorganisms have been comprehended mainly as cosmopolitans, thus exhibiting low beta diversity due to their small size and huge population densities (e.g. Finlay 2002). However, recent studies have shown that microbial organisms, including many aquatic taxa, may show restricted distributions at large spatial scales (e.g. Green et al. 2004, Vyverman et al. 2007, Evans et al. 2009). Macroecological patterns for microorganisms should thus be properly contrasted with the patterns observed for macroorganisms to resolve whether there are common constraints for all life forms.

Besides affected by species traits, variation in community composition is also set by the spatial scale of the observations (Soininen et al. 2007*a*). The spatial structure of the communities should be stronger (i.e. beta diversity higher) at large spatial scales where dispersal limitation may act more strongly, and environmental gradients are longer (Rosenzweig 1995, II). At large scales, communities may be even more strongly structured by dispersal-related processes, evolution and historical factors than by local environmental conditions and interactions (Vyverman et al. 2007). On the contrary, dispersal should be efficient between local communities at small spatial scales due to the lack of dispersal barriers. The lack of barriers can result in weak spatial structure (i.e. low beta diversity) of the communities and local community control by environmental filtering and biotic interactions.

In addition to species dispersal ability and spatial scale, the degree of beta diversity in communities may be affected e.g. by latitude and ecosystem type (Soininen et al. 2007a).

1.3. Factors affecting communities in time

Spatial variation in communities is but one aspect of beta diversity. The second component is variation in communities through time – temporal beta diversity, i.e., temporal turnover. Studies examining spatial turnover are more common than

papers addressing temporal community patterns due to demand for long-term data, which are not easily available (Magurran et al. 2010). However, studies on turnover in time do suggest that the degree of temporal turnover can vary systematically across organisms and ecosystems.

Like spatial variation in species composition, temporal turnover is likely to be driven by multiple factors. One of the most evident factors driving the variation in assemblage composition through time is the temporal extent of the study, that is, how long a certain area is sampled. It has been suggested that there is a species-time relationship (STR) comparable to the species-area relationship (SAR), i.e., the longer an area is sampled, the more species are observed, but at a decreasing rate with increasing temporal duration.

Processes behind the STR (or equivalently, temporal turnover) are somewhat unkown, but these can be classified into three major categories: sampling effect, ecological and evolutionary factors (Rosenzweig 1995). At short timescales, the patterns in turnover are mostly driven by the sampling effect as ecological or evolutionary factors rarely have enough time to shape the assemblage at such short timescales. At intermediate timescales, however, temporal turnover is shaped also by ecological processes, such as local colonization and local extinction that are driven by temporal variation in the environment or dispersal patterns across sites. At long timescales, evolutionary processes such as speciation and extinction tend to dominate the increase in species richness in the sampling area.

As the sampling of most biological data covers intermediate timescales (from weeks to years), the variation in the rate of turnover should be affected not only by sampling effect, but also by various ecological factors. Turnover is expected to get slower with the increasing **sampling duration** because detecting new species becomes slower when the temporal extent of the study increases (Preston 1960, Anderson 2007, Fig.2). The most abundant species are detected first, and as sampling continues, rare species will also be sampled. Second, the rate of turnover is related to **ecosystem size**, with larger ecosystems showing lower turnover rates (Adler et al. 2005). It has also been suggested that the degree of temporal turnover is driven by the **ecosystem type**. Marine ecosystems are expected to be much larger and physico-chemically more stable than lakes or streams. According to the species-time-area relationship (STAR; Adler et al. 2005), marine assemblages should have slower turnover than freshwater assemblages because of larger ecosystem size.

Fourth, temporal turnover may also show **large-scale geographical variation.** As low latitudes are characterized by high energy input directly affecting the organisms` rate of life cycle, faster temporal turnover in tropics is expected (reviewed by Brown et al. 2004). On the other hand, high latitudes are usually characterized by strong seasonality, which may lead to faster temporal turnover toward poles especially at the short timescales. Fifth, temporal turnover can also be related to **organisms` intrinsic properties**. In contrast with the larger organisms, microbial eukaryotes (e.g. protozoa and microalgae) and prokaryotes have extremely high cell densities and

small body size showing high turnover in time.

Temporal turnover and body size may be linked by at least two processes. Firstly, the rate of life cycle is directly linked to body size through metabolic constraints (Brown et al. 2004). Second, small organisms probably show fast fluctuations in population dynamics as they have large species pools from where local sites can be rapidly colonized thus exhibiting fast turnover. Therefore, larger organisms can exhibit slower temporal turnover than the smaller organisms.

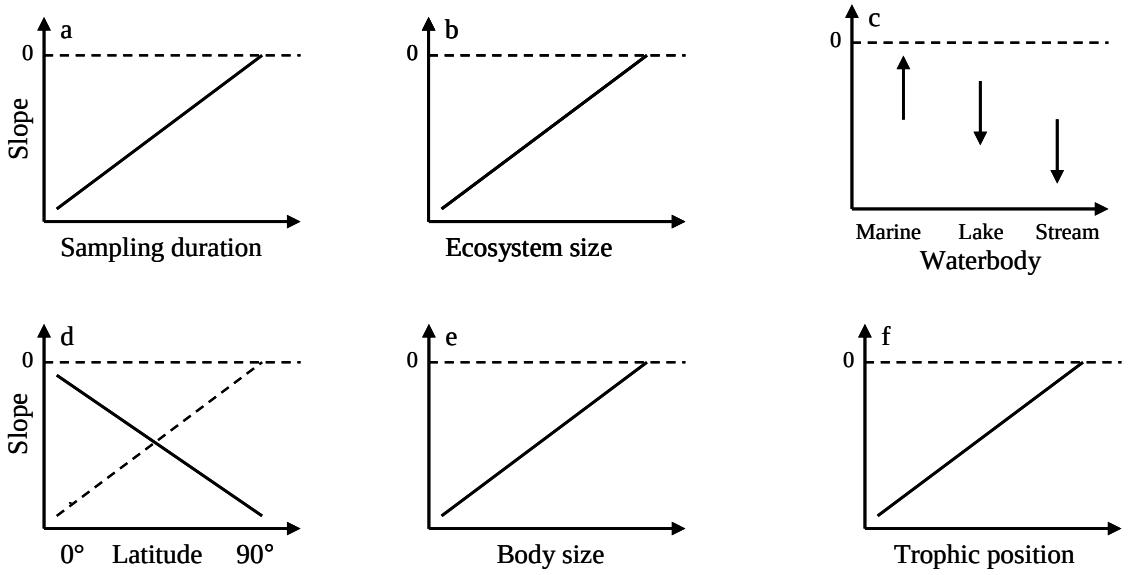

Figure 2. A conceptual figure outlining the predicted changes in slope of the linear regression between community similarity and time across (a) sampling duration, (b) ecosystem size, (c) type of waterbody, (d) latitude, (e) organism body size, and (f) trophic position in a food web. The values of the slopes are negative. When the slope approaches zero, turnover slows down. Specific predictions are: (a) turnover slows down with the increasing sampling duration of the study, (b) turnover slows down with the increasing ecosystem size, (c) rate of turnover varies significantly among the different waterbodies and turnover is slowest in marine ecosystems, (d) rate of turnover decreases or increases with the latitude, (e) turnover slows down with the increasing body size, and (f) turnover is faster at the low trophic position in a food web. (III)

1.4. Plankton communities

The main organism group studied in this thesis is freshwater plankton. It comprises multiple trophic groups (i.e. bacteria, algae and small invertebrates) living freely in the open water. The main features of these groups are presented in the next chapters.

1.4.1. Bacterioplankton

In aquatic ecosystems, bacteria play a fundamental role in nutrient cycling and energy fluxes (Wetzel 2001). Although the functioning of aquatic ecosystems are controlled by the metabolic transformations of organic matter by bacteria (and fungi), the studies of aquatic bacterial communities have not been a major research topic in aquatic ecology so far.

Planktonic bacterial communities are usually limited by the availability of organic substrates for assimilation of nutrients, specifically phosphorus and nitrogen (Wetzel 2001). Second, environmental factors such as temperature and ultraviolet (UV) light can affect bacterial growth. In general, the number and biomass of bacteria increase with increasing productivity and inorganic/organic compounds in the water body. In natural bacterioplankton communities, bacterivory by protists and larger zooplankton is the major mortality factor (Wetzel 2001). Bacterivory is dominated by heterotrophic nanoflagellates. In addition, *Daphnia*, *Bosmina* and other cladocerans are seasonally effective in consuming the bacterioplankton, during the "clearwater phase", for example. Moreover, in eutrophic lakes where bacterial growth rates and production are high due to the elevated amount of nutrients and organic carbon, the relative significance of cladoceran bacterivory can increase (Pace & Cole 1996).

1.4.2. Phytoplankton

The phytoplankton, i.e. the algae living in the open water, consists of a large number of species from nearly all major taxonomic groups of algae (Wetzel 2001). These forms have different physiological requirements and their responses to physicochemical conditions, such as light, temperature or nutrient input, vary substantially. Cyanobacteria (blue-green algae) are prokaryotes capable of photosynthesis and they are a major part of the phytoplankton. In this thesis, cyanobacteria are treated as functionally similar to the other planktonic species although they are capable of fixing nitrogen from the air. The Chlorophyta (green algae) are a morphologically diverse and numerous algae group that is present mainly in freshwaters. Most planktonic Chlorophyta belong to the orders Volvocales and Chlorococcales (Lee 2008).

The yellow-green algae (Xanthophyceae) are characterized by carotenoids, which produce in their coloration. A few yellow-green algae are planktonic, such as genera *Chlorobotrys* and *Gloeochloris*. The golden-brown algae (Chrysophyceae) are an important part of the phytoplankton with a distinctive golden-brown coloration caused by the dominance of β-carotene and xanthophyll carotenoids in their chromatophores (Lee 2008). Unicellular species, such as generas *Chromulina* or *Mallomonas* are

usually representatives of the nanoplankton. Larger colonial forms (e.g. *Uroglena* and particularly *Dinobryon*) are widely distributed and sometimes extremely abundant in certain environmental conditions, for instance in temperate oligotrophic lakes (Hutchinson 1967). Cryptomonas are a small class of mostly naked, unicellular and motile microflagellates. Also the dinoflagellates (Dinophyceae) are flagellated and usually motile, naked or armored types occur. The euglenoids (Euglenophyceae) are a large and diverse group, yet few species are planktonic.

Probably the most important group of algae is the diatoms (Bacillariophyceae). Although most diatoms are sessile and associated with littoral substrata, they are an important component of the phytoplankton because of their high cell densities and high diversity. Their primary characteristic is the silicified cell wall.

Phytoplankton ecology is one of the most popular research areas in modern aquatic ecology and many breakthroughs have been made for instance in understanding productivity, light, nutrients and temperature requirements and effects of predation on phytoplankton (Wetzel 2001). However, further investigation is urgently needed, especially in the areas of interactions between microbes, algae and herbivores.

1.4.3. Zooplankton

Compared to the diversity of the phytoplankton, the diversity of planktonic microscopic animals, i.e. the zooplankton, is relatively low (Wetzel 2001). The zooplankton is dominated by four major groups: 1) Protists (Protozoa and heterotrophic flagellates) are the most important microbial consumers and they have major roles in organic carbon utilization and nutrient recycling. 2) Rotifera, or rotifers, pseudocoelomate animals, such as genera *Synchaeta* and *Keratella* are found in a wide variety of environments 3) Cladocerans are usually small (0.2-3 mm in length) and have a distinctive head. Large second antennae are used on locomotion. Most cladocerans feed on filtered particles but a few are predaceous. 4) Planktonic Copepoda consists of two major groups: the calanoids and the cyclopoids. Calanoids have a capability to swim continuously in rotary motions which set up currents that carry food particles to the maxillae. However, cyclopoids are raptorial, many of them being carnivorous on other zooplankton although some are herbivorous.

1.5. Lakes, ponds and streams as study systems

One of the most interesting ecosystems for studying the temporal and spatial patterns in species assemblages are small freshwater lakes and ponds scattered in a terrestrial landscape. Small lakes and ponds form distinct habitat patches, which are often only connected by the overland dispersal of organisms (Wilbur 1997). Besides dispersal limitation, local environmental factors are important as well. Lakes and ponds range along a major gradient from fish-free habitats to fish-rich water bodies, and from ultraoligotrophic to highly productive waters (Wellborn et al. 1996). Plankton communities are an important component of the biota in all lakes and

ponds and even tiny ponds may house surprisingly diverse plankton communities (Soininen et al. 2007*b*).

Studies on the planktonic organisms in ponds and small lakes have focused on the role of local environmental factors. Recent papers on lake plankton communities suggest, however, that planktonic communities are structured both by environmental and spatial variables (Beisner et al. 2006, Langenheder & Ragnarsson 2007). The extent to which environment and space drive patterns for planktonic groups of different size, at different trophic levels and spatial scales are still poorly understood. Therefore, inter-taxonomic group comparisons across multiple spatial scales should be optimal for a deeper understanding of community organisation among different taxa.

Streams are another central component of aquatic ecosystems. The continuous and directional movement of water in lotic (i.e. flowing) freshwaters is their fundamental property as it affects e.g. the water chemistry, morphology of the stream, biology of the inhabiting organisms and sedimentation patterns (Allan & Castillo 2007). Streams are usually more prone to disturbances than stagnant waters. Fluctuations in discharges can cause major changes in water chemistry and physical characteristics of the stream.

Given that lakes and streams represent highly different ecosystems for aquatic organisms to live in, they present excellent opportunities to examine the differences in major community patterns and drivers between these ecosystems.

1.6. The main objectives of the study

1. To investigate productivity-diversity relationships in three planktonic groups (bacterio-, phyto- and zooplankton) at two spatial scales (within and across drainage systems). (I)

2. To study the relationships between resource availability, species richness, biomass and resource ratio (N:P) in phytoplankton communities. (I)

3. To compare spatial patterns in community composition of the three different planktonic groups at two spatial scales. (II)

4. To study the patterns in temporal turnover of aquatic species assemblages in relation to several ecological, physical and geographical factors. (III)

5. To study the temporal variation in lotic diatom communities within a year and between three years in streams of different trophic levels and sizes. (IV)

2. MATERIAL AND METHODS

2.1. Study area

2.1.1. Papers I-II

Bacterio-, phyto-, and zooplankton samples were collected once from 100 small lakes in Finland during July in 2008 and 2009. The sites were sampled at five drainage systems, 20 lakes per system. In 2008, we sampled 60 lakes at three drainage systems and in 2009 40 lakes at two drainage systems. The sampled drainage systems were (1) Vantaanjoki, (2) Karjaanjoki, (3) Kokemäenjoki, (4) Upper Kymijoki, and (5) Koutajoki (Fig. 3).

2.1.2. Paper IV

Diatoms were sampled at eight stream sites located in southern Finland (Fig. 4). The diatom samples were collected at each site nine times per summer in years 2006–2008. Four of the sampling sites were located in eutrophic River Vantaanjoki and the four others were located in oligotrophic Rivers Evojoki and Luutajoki.

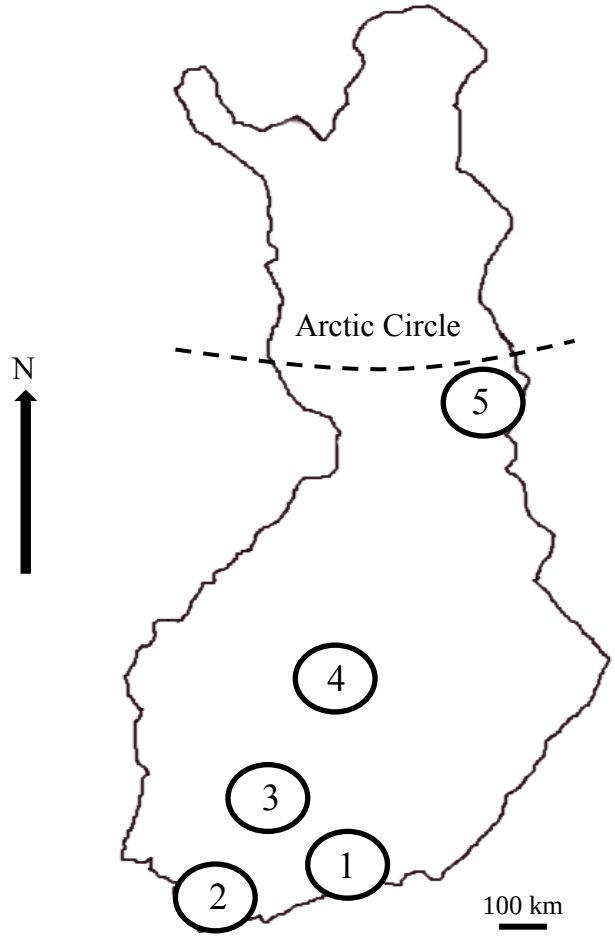

Figure 3. Map of Finland with the study areas marked by gray circles. The study areas were: 1) Vantaanjoki, 2) Karjaanjoki, 3) Kokemäenjoki, 4) Upper Kymijoki, and 5) Koutajoki (papers I-II).

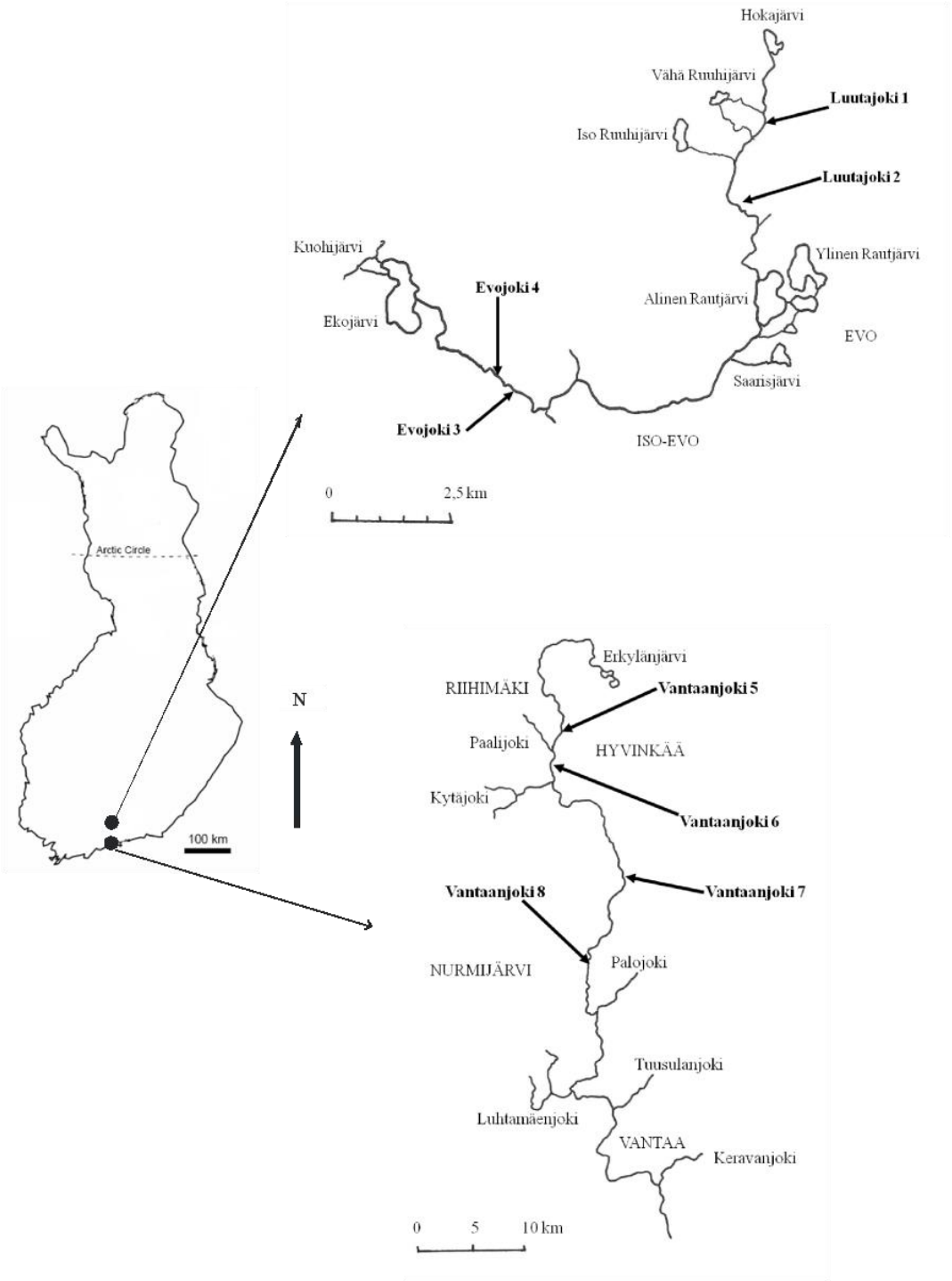

Figure 4. Map of Finland and locations of sampling points in Rivers Evojoki, Luutajoki and Vantaanjoki (IV).

2.2. Data collection and sample processing

2.2.1. Papers I-II

Phytoplankton and zooplankton samples were collected with a tube sampler. Phytoplankton subsamples were mixed and fixed immediately with acid Lugol´s iodine solution. Zooplankton samples were filtered through a 50 µm net and preserved with formaldehyde in the field. 250 mL of water was filtered through a 0.42 µm pore-sized nitrocellulose filter to remove larger particles. Bacteria cells were then collected on a 0.22 µm pore-sized nitrocellulose filter, which was frozen immediately in the field. The maximum depth of the lakes as well as surface water temperature was measured. I included water temperature as an explaining variable in the data because it showed notable differences among the sampled drainage system. The area of each lake was measured using GIS.

Samples for water chemistry analyses were collected simultaneously with the plankton sampling and analyzed in the laboratory for conductivity, chlorophyll *a*, color, total nitrogen, and total phosphorus using national standards.

2.2.2. Paper III

The data comprised studies that report raw data (i.e., species composition and abundances in tables or figures) on how species assemblages change through time. In total, I scanned through ca. 2500 papers of which we chose 99 papers or unpublished studies concerning aquatic assemblages into closer examination. From these, I obtained 383 distance decay relationships in time, that is, relationships that describe how assemblage similarity decreases with time.

The relationships were classified with respect to four continuous variables (organism body size, latitude of the center of a study area, ecosystem size and sampling duration), and four categorical variables (organisms' trophic position, dispersal type, habitat and type of waterbody).

I divided papers into intra-annual (< 365 days) and interannual (≥ 365 days) studies. In a few cases, long-term sampling of organisms that are primarily annual was interrupted by winters at high latitudes. For example, in long-term phytoplankton studies at high latitudes, samplings occurred typically only during summers. In these cases, data were treated as separate intra-annual studies.

Organism body size was approximated as log-transformed wet weight (g), and derived for each organism group from Peters (1983). Latitude was scored from 0 to 90, with no distinction between the northern and southern hemisphere. Ecosystem sizes for marine studies were drawn from the papers or calculated using the areas of the whole ecosystem (e.g. North Atlantic). Lake and pond sizes were derived from original papers or by calculating areas using maps of the original studies. Ecosystem sizes (in hectares) were log-transformed.

Temporal duration of the analysis was measured in days and was log-transformed. The habitat was divided into nekton, plankton or benthos. I classified organisms by their dispersal ability into four categories: mobile (e.g. fish), pelagic larvae (e.g. corals), spores (e.g. macroalgae) and passive (e.g.

microalgae). Finally, the type of waterbody was divided into streams, lakes and marine ecosystems.

2.2.3. Paper IV

In paper IV the samples were collected at each site nine times per summer in years 2006–2008. Sampling days were chosen so, that starting from the 1st of June the summer was divided in periods of 20 days. Between every 20 days sampling period there was a gap of 20 days in the sampling. For every three periods, three sampling days were randomly picked. For sampling, each riffle was divided into ten cross-sections at intervals of one meter. Ten stones were picked from these sections, one per each section. Diatom samples were collected semi-quantitatively from the stones by using a toothbrush and a soft rubber template, in which a hole of a 9 cm^2 was cut. An equivalent sample was brushed from each stone and all the ten samples were pooled into one sample container.

Simultaneously to diatom sampling, pH, conductivity and temperature were measured at the stream sites. In addition, average current velocity, water depth, stream width, slope and shading by the canopy was determined. Depth (cm) and current velocity (cm/s) were measured at 40 random locations along the same transects where we picked up the sampling stones. To measure the current velocity we used a flowtracker. Stream slope (cm/10 m) was determined using a carpenter´s level. Shading (% canopy cover) was estimated visually using a cylinder at 20 random locations along transects. At each sampling site, one 500 ml water sample for total P and N analyses and one 250 ml sample for the water color analyses were collected.

2.3. Laboratory analyses

2.3.1. Papers I-II

In the laboratory, the phytoplankton samples were concentrated using Utermöhl chamber counter with a light microscope (magnification 400x). For zooplankton, all individuals were counted from the whole chamber area at magnification of 125—400x using an inverted microscope. Potential ecosystem productivity was assessed using concentrations of chlorophyll *a* (biomass production) as well as total P and total N (resource supply). N:P ratio was used as a surrogate for resource ratio.

2.3.1.1. Nucleic acid extraction and PCR for bacteria

Nitrocellulose filters (25mm) were cut in half and placed into a 1.5mL microtube which was then dipped in liquid nitrogen. The filters were then roughly ground with a plastic pestle and DNA was extracted with a protocol of Griffiths et al. (2000, for details, see papers I-II) For the tRFLP analysis (Liu et al. 1997), PCR amplification of 16S ribosomal genes for tRFLP was achieved by using primers FAM-E8F (FAM-5'-AGAGTTTGATCCTGGCTCAG-3') and E939R (5'-CTTGTGCGGGCCCCCGTCAATTC-3') (Baker et al. 2003) with reaction conditions optimized for the enzyme DyNAzyme II (Finnzymes, Espoo Finland). PCRs were run in triplicate reactions, aliquots were checked by

agarose gel electrophoresis separately and the rest of the volume was pooled. The pools were purified with a Millipore Multiscreen plate. The clean PCR products were digested with 5 units of restriction enzyme (HhaI, Fermentas) for 18 hours in duplicate reactions. Dilutions of the digested and undigested samples were run on an ABI 3130xl device at 60°C. The resulting peak profiles were analyzed using the ABI PeakScanner software. All peaks with a size of 50-940bp and a relative height of at least 0.1% present in both digestions were manually recorded for each sample and compared to profiles from undigested PCR products.

2.3.2. Paper IV

Organic substance was removed from the diatom samples by adding hydrogen peroxide (30 % H_2O_2) and boiling the samples until the organic substance oxidized. Cleaned diatoms were mounted in Naphrax®. A total of 500 frustules per sample were identified using the nomenclature of Krammer and Lange-Bertalot (1986-1991) and counted using phase contrast light microscopy (magnification 1000X).

2.4. Data analyses

2.4.1. Paper I

The relationship between species richness and nutrient supply (i.e. concentrations) was analyzed using linear and quadratic regression with AIC (Akaike´s Information Criterion) to select the best model. The relationships were analyzed at two spatial scales: within and across the drainage systems.

Moreover, I used regression analysis to test the relationship between phytoplankton species richness and biomass. Analyses were done using SPSS 15.0. I also studied if phytoplankton community composition was related to phytoplankton biomass. This was done by regressing site NMDS (Non-Metric Multidimensional Scaling) 1 scores against phytoplankton biomass of a site. NMDS analysis was conducted using presence-absence data of the phytoplankton species with the R package 2.8.

The relationships between resource ratio (N:P), resource availability, species richness and phytoplankton biomass were examined using Structural Equation Modeling (SEM, Grace 2006). Total N and total P values were standardized to have a mean of zero and standard deviation of 1. The resource availability (a) and resource ratios (θ) were calculated using resource vectors from the two resource values (total N and total P) according to equations 2 and 4 in Cardinale et al. (2009). The goodness of fit of the full model was tested using Chi-square test. Akaike´s Information Criterion (AIC) was used to select the most parsimonious model. Using AIC, the final model was chosen based on the likelihood (AIC_L) that the model was the best fit to current data set among the candidate models. A full path model without model selection was conducted to show all related individual pathways. SEM was conducted in Amos 18.0.

Finally, I studied which environmental, geographical or biological factors were strongest determinants of species richness for

each planktonic group. I calculated the relationship between species richness and water chemistry (total P, total N, color, conductivity), water temperature, surface area, maximum depth and geographical location (latitude and longitude) of the lake using GLM with the best model selection by AIC. As the PDR is frequently unimodal, I also included the second order terms of total P and total N in the candidate models. The cross-taxon concordance between zooplankton, phytoplankton and bacterioplankton richness was analyzed including richness values into GLM models as well as with the separate correlation analyses. Analyses were conducted using R package 2.8.

2.4.2. Paper II

Redundancy Analysis (RDA) was used to explore the main patterns in community composition of the planktonic groups and to relate these to environmental and spatial variables. RDA with forward selection was run for the whole set of lakes (n=100) for each planktonic groups. Amount of chlorophyll *a* was not included in RDA analysis for phytoplankton.

Mantel test with Pearson correlation coefficient was used for each data set to examine the patterns in community similarity along environmental and geographical distance within and across drainage systems (Legendre and Legendre 1998). Distance matrices were produced for environmental, geographical, and biological data. Environmental variables and site coordinates were centered on their respective means and standardized by standard deviate, and among-site Euclidean distances were then calculated between all site pairs separately for data of environmental variables and site coordinates. In species data, Sorensen coefficient was used to calculate the pairwise similarities.

Initial similarity and halving distance for the distance-decay relations were calculated at across-drainage system scale. First, the similarity was calculated at one km distance (initial similarity), which describes species turnover at small scales. Initial similarity was computed as Sim (1) = $\beta*1 + \alpha$, where β and α are the regression parameters for the slope and intercept. Second, we calculated how much further apart sites would have to be to halve the similarity at one km distance - the halving distance. For the linear-linear regression form, the halving distance is given as $(\beta - \alpha) / 2\beta$.

Moreover, partial Mantel tests were conducted. Partial Mantel test examines the influence of environmental distance on biotic distance while controlling for geographical distance and vice versa. The significance of the correlations between similarity and distance was assessed using 1000 randomizations. Mantel tests were conducted using package Vegan in R (Oksanen et al. 2006).

We then tested whether the sampled drainage systems harboured significantly different community compositions of all planktonic groups using Multi-Response Permutation Procedures (MRPP) (Berry et al. 1983). The significance of the null hypothesis of no difference among the groups was assessed by a Monte Carlo randomization procedure with 1000 permutations. MRPP was run using package Vegan in R.

Finally, Mantel test was used to examine whether planktonic groups show significant concordance in their community composition. Significant concordance would indicate that if two lakes harbour similar bacteria composition, for example, these lakes would also harbour similar phytoplankton and/or zooplankton composition. Sorensen coefficient and 1000 randomisations in package Vegan in R were used.

2.4.3. Paper III

I calculated the relationship between assemblage similarity and distance in time from each pair of observations. I regressed assemblage similarity and temporal distance and obtained the slope of the linear regression as an indicator for the rate of temporal turnover. Slope was measured as a decrease in assemblage similarity per year. Steeper slope (i.e. more negative) indicate faster temporal turnover, whereas a slope = 0 indicates no turnover in time. Although the pairwise comparison of data points inflates N, the estimate of the slope is not inflated.

I used General Linear Model (GLM) with the selection of the best model to unite the effects of categorical and continuous variables on temporal turnover. GLM for intra-annual (n = 280) and interannual studies (n = 103) was performed separately. The most parsimonious models were identified using Akaike`s Information Criterion (AIC, Burnham and Anderson 1998). The General Linear Model was conducted using R package.

2.4.4. Paper IV

Non-metric Multidimensional Scaling (NMDS) was used to describe the temporal variation in diatom community structure between the years. Sorensen's distance measure was used for all analyses.

The statistical significance of differences between the community compositions among the sampling years was tested using Multi-Response Permutation Procedures (MRPP; Berry et al. 1983). NMDS and MRPP were conducted using the program PC-ORD version 4 (McCune & Mefford, 1999).

The relationship between community similarity and distance was calculated in time for each pair of observations. This was done to examine how fast community similarity decayed in time at each site within the sampling years. The statistical significance of the relationships was determined using Mantel test with 999 random permutations. Correlation coefficient (Mantel r) was used as an indicator for temporal variation. T-test was used to compare the correlation coefficients between the streams. Sorensen coefficient was used as a similarity metric.

3. RESULTS

3.1. Productivity-diversity relationships in lake plankton

At within-drainage system scale, the PDR showed highly variable patterns in all organism groups ranging from positive linear and unimodal relationships with total P to negative

linear relationships in some of the drainage systems (for details, see I).

Across regions comprising all 100 lakes that were sampled, there were significant linear relationships between log-transformed phytoplankton and zooplankton species richness and total phosphorus (R^2 = 0.237; P = 0.001, R^2= 0.067, P = 0.009, respectively). Bacterioplankton richness did not show a significant relationship with total P. Given that I found linear relationships across drainage systems covering the larger study scale, but variable patterns within the drainage systems, these results give overall partial support for the scale-dependency of the PDR in our study system.

Phytoplankton richness and the amount of chlorophyll *a* (µg/l) showed a positive linear relationship (R^2 = 0.068, P = 0.009) across the whole set of lakes. This may indicate that the communities consisting of higher number of species were able to produce higher levels of biomass from basal resources. It also seems that community composition has either direct or indirect effects on standing biomass, as community composition (summarized by NMDS 1 scores) was related to phytoplankton biomass (R^2=0.121, P<0.001).

In the SEM analysis for phytoplankton data, phytoplankton biomass was largely related to resource availability, yet there was also a pathway via community richness (Fig. 5, I). Surprisingly, there were no significant effects of resource availability on richness and resource ratio on richness in this model. However, full path model without the model selection showed a significant effect of resource availability on richness (coefficient = 0.10). Overall, the best multivariate model explained 32 % of the variation in phytoplankton biomass.

Finally, I studied whether planktonic richness was related to some other physicochemical factors, location of the lake or richness of the trophic levels other than the focal planktonic group. The most parsimonious model for the whole zooplankton data included three variables (water temperature, bacterioplankton and phytoplankton richness), which were all positively correlated with zooplankton richness explaining 21% of the variability in richness. For the phytoplankton, conductivity, longitude, total N, and zooplankton richness showed positive relationships with phytoplankton richness, while latitude and phytoplankton richness were negatively correlated. The five variables jointly explained 48% of the variation in phytoplankton richness. Variation in bacterioplankton richness, in turn, was mainly related to geographical position of the lake and zooplankton richness. Longitude was negatively correlated, while latitude and zooplankton richness showed positive correlations with bacterial richness. The three variables jointly explained 15% of the variation in bacterioplankton richness.

3.2. Spatial patterns in community composition

For the whole set of lakes, RDA for bacteria indicated that the first main gradient was best related to water temperature, surface area of the lake, depth and trophic status of the lake. The second main axis was mainly related to water colour and latitude. RDA for phytoplankton indicated that the first main gradient was best related to total P, water colour and geographical position of the lake (Fig.

5b, paper II). The second main gradient was mainly related to surface area of the lake and the geographical position of the lake. RDA for zooplankton indicated that the first main gradient was mainly related to amount of chlorophyll *a*, water colour, latitude and total P (Fig. 5c, paper II). Second RDA axis in turn was best related to water temperature and geographical position of the lake.

Mantel tests showed that community similarity of bacteria was not significantly negatively correlated with geographical or environmental distance within any of the studied drainage systems (Table 3, paper II). However, pairwise community similarity showed significant negative correlation with geographical distance across the whole set of lakes. However, there was no correlation between community similarity and environmental distance even if all lakes were considered. The halving distance was longest and initial similarity lowest for the bacteria.

For phytoplankton, the negative correlations between community similarity and environmental distance were significant at all drainage systems. Phytoplankton also showed strong correlations between community similarity and geographical distance and between similarity and environmental distance across the whole set of lakes. The halving distance was nonetheless long along with high initial similarity. Phytoplankton did not show any significant spatial distance decay within the drainage systems.

Zooplankton showed significant negative correlations between community similarity and environmental distance in two regions. However, community similarities were not related to geographical distance in any of the regions. Across the whole set of lakes, zooplankton showed strongest correlation between community similarity and geographical distance of the three planktonic groups. Strong spatial distance decay was also reflected as highest slope and shortest halving distance.

MRPP showed that the sampled drainage systems harboured significantly different communities for all planktonic groups. The A-statistics indicated that zooplankton showed highest within-group similarity, i.e., the drainage systems had more homogeneous communities of zooplankton than of phytoplankton or bacteria.

According to Mantel test, phytoplankton and zooplankton showed significant concordance in their assemblage patterns. Other pairwise comparisons between planktonic groups were non-significant.

A total of 97 different tRFLP peaks from the 100 surveyed lakes were identified with single samples comprising from 3 to 25 peaks. The OTU count between drainages varied from 32 to 58 and the more urbanized environment (Vantaajoki drainage system) had the lowest average richness across all lakes and lowest total amount of peaks among the regions.

I detected 238 phytoplankton taxa in the data. The most numerous phytoplankton taxa belonged to the division Cyanobacteria (Cyanophyceae). The most common genera were *Anabaena*, *Aphanocapsa*, *Aphanothece*, *Chroococcus*, and *Snowella*. Species from the phylum Cryptophyta were also abundant. The most numerous genera were *Cryptomonas* and *Rhodomonas*. Of

the sampled regions, the largest number of phytoplankton taxa (135) where found in Vantaanjoki drainage system.

In total, I found 64 zooplankton taxa. The number of local taxa in lakes ranged from 2 to 16. The total number of taxa ranged from 31 (Upper Kymijoki) to 46 (Karjaanjoki) among the drainages. The most numerous zooplankton taxa represented the order Cladocera. The most common species were *Bosmina coregoni* and *B. longirostris* (Bosminidae) and several species from the family Daphniidae. The most common daphnids were *Daphnia cristata, D. cucullata* and *Ceriodaphnia pulchella*. Rotiferans were also rather common. *Kellicottia longispina*, *Keratella cochlearis* and *Polyarthra remata* were the most common rotiferan species.

3.3. Temporal turnover in aquatic species assemblages

3.3.1. Intra-annual studies

The average slope for the intra-annual studies was -1.02 (± 0.009 S.E.). This means that the whole assemblage turns over within a year. The sampling duration was strongly positively correlated with the slope, as we predicted (Table 2, III). Thus, when the sampling duration increases, temporal turnover slows down (= less negative slope). Latitude also showed a positive relationship with the slope implying that the turnover was faster in tropics than in assemblages at high latitudes. Moreover, the results suggest that temporal turnover was faster in benthos than in plankton

3.3.2. Interannual studies

Mean slope of the interannual data set was -0.095 (± 0.10 S.E.) and it was significantly smaller than in the intra-annual data set ($t = 9.13$, $p < 0.001$). The average slope means that 9.5% of the assemblage turns over between years.

Sampling duration showed a positive relationship with the slope, as was predicted (Table 2, III). Thus, temporal turnover decreased with the increasing sampling duration. Contrary to what was predicted, ecosystem size showed a negative relationship with the slope implying that turnover was faster in larger ecosystems.

The degree of turnover also varied consistently across the waterbodies (Table 2, III). Lake ecosystems showed the fastest turnover, and marine and lotic assemblages showed much slower average rates of temporal turnover. The long-term turnover also showed large-scale geographical variation as latitude was negatively related to slope suggesting faster temporal turnover towards the poles.

Moreover, I found that the interannual turnover was also related to organism characteristics. Body size showed a positive relationship with the slope, as I predicted, indicating that the larger organisms have slower temporal turnover. Temporal turnover was also related to dispersal as it varied significantly between the dispersal types. Mobile organisms and organisms with pelagic larvae had the slowest temporal turnover. Passively dispersing organisms and organisms dispersing by spores had the fastest turnover.

3.4. Variation in diatom assemblages

3.4.1 Between-year variation in assemblages

According to NMDS analyses, assemblages varied widely between the sampling years (Figs. 3-5, paper IV). Based on NMDS analysis conducted simultaneously for the whole diatom data, oligotrophic Rivers Evojoki and Luutajoki were clearly separated from the eutrophic Vantaanjoki in ordination space (Fig. 3, paper IV). When samples were grouped according to year, higher A value (A = 0.071) indicated that River Vantaanjoki showed more different assemblage compositions between the years than Rivers Evo- and Luutajoki (A = 0.039, Fig. 3a). However, when grouping was based on sampling sites, Rivers Evo- and Luutajoki showed more distinct assemblage compositions (A = 0.184) while sites in River Vantaanjoki showed a higher degree of overlap (A = 0.081, Fig. 3b, paper IV).

MRPP analyses indicated that the assemblage composition differed statistically significantly among the three years at all sites ($P < 0.001$) (Figs. 4-5, paper IV).

3.4.2 Within year variation in assemblages

According to Mantel tests, there were no statistical differences in within-year variation in diatom assemblages between River Vantaanjoki and Rivers Evojoki and Luutajoki as Mantel r values did not differ from each other (ANOVA, P = 0.8). The r values were, however, overall slightly higher in Rivers Evojoki and Luutajoki (Fig. 6, paper IV).

4. DISCUSSION

4.1. Alpha diversity: Productivity-diversity relationships in plankton

Regardless of the great potential of lakes for studying PDRs, I found large variability in the PDR among the five drainage systems for all planktonic groups. As multiple ecosystem processes may act simultaneously, I studied the concomitant pathways between phytoplankton richness, resource availability, resource ratio and biomass. A strong pathway between resource availability and biomass was found, but I also found an indication that higher richness resulted in higher algal biomass. I further studied if species richness is correlated with some other factors than mere productivity of a lake. E.g. for zooplankton, water temperature was positively correlated with species richness. Also, I found a concordant relationship in richness between zooplankton and phytoplankton and between phytoplankton and bacterioplankton diversity.

Variability among the PDRs is in line with Witman et al. (2008) who also found variable PDRs in Arctic macrozoobenthos indicating that PDRs may often be highly context dependent. The reason for the lack of clear PDR within drainage-systems remain speculative at present but may be related to the facts that (i) planktonic organisms were overall

largely driven by some other factors than productivity and (ii) productivity gradients were not long enough for producing a "hump-shaped" PDR in these unmanipulated systems. However, I emphasize that e.g. the study by Chase & Leibold (2002) on scale-dependency in PDRs was conducted at much smaller spatial extent than our study as they compared PDRs within a single pond with PDRs among multiple ponds sampled in one drainage system only (versus 20 lakes sampled in five drainage systems as were considered here). They collected samples twice per year, over two years. Therefore, their findings are not fully comparable to present results because of substantially larger spatial scale in the present study and different amounts of sampling occasions.

The finding on the indirect pathway between phytoplankton resource availability and biomass through richness suggests that higher richness is related to more efficient ecosystem production. Cardinale et al. (2009) have proposed that as resources become increasingly imbalanced, biomass production slows down. However, a positive effect of resource ratio on biomass was found here, but no strong pathway between resource availability and species richness.

The positive relationship between zooplankton richness and temperature may stem from higher energy-input supporting more species as predicted by the species-energy theory (Currie 1991, Hillebrand 2004). Moreover, as bacterioplankton and zooplankton richness are positively related, that means that the positive feedbacks between trophic levels can maintain species diversity in these communities. Positive correlations in richness between the trophic levels have been found in several studies of terrestrial systems (Van der Heijden et al. 1998, Haddad et al. 2001, Hawkins & Porter 2003), but in aquatic ecosystems correlations in richness across trophic levels have been weak or non-significant (Allen et al. 1999, Irigoien et al.2004, Longmuir et al. 2007).

Due to these disparate results, it has been suggested that the degree of concordance in species richness patterns among trophic levels generally differ between terrestrial and aquatic systems (Longmuir et al. 2007). It may be that the major environmental factors affecting species richness are different for each trophic level. One may suggest that the similar accumulation of species across trophic levels may be driven by species interactions between trophic levels in the planktonic food web rather than similar responses to environmental gradients.

4.2. Beta diversity: Community composition in plankton

The lake bacteria did not show any correlations between community similarity and geographical or environmental distance within drainage systems. However, bacterial community similarity decreased with geographical distance when the spatial scale extended to cover the five studied systems. Phytoplankton communities were related to local environmental factors within drainage systems while other communities showed only weak relationships with environmental variables. I further found that zooplankton showed strongest spatial distance decay among the planktonic groups as was predicted (paper II).

First, results show that bacteria are probably not severely dispersal limited within the drainage systems nor do

they relate to environment at small scales, but they nonetheless responded to environmental variables at across-system scale. This suggests that the variation of bacteria community composition can be influenced to some extent e.g. by water colour (indicating mostly the amount of DOC in lakes), trophic status of the lake and available energy in terms of water temperature with some additional effects by geographical position and surface area of the lake. The influence of water colour was revealed already by Beisner et al. (2006) and Langenheder and Ragnarsson (2007) who emphasized the effect of carbon supply on lake bacteria communities. Moreover, Van der Gucht et al. (2007) identified water temperature as one of the main drivers of bacteria community composition in lakes in Spain and surface area in lakes in Belgium, Netherlands and in Denmark.

Second, the bacteria are spatially structured at large scales which means that even the microscopic organisms may show biogeographical patterns at large scales (Green et al. 2004; reviewed in Martiny et al. 2006). However, compared with phyto- or zooplankton, correlation between geographical distance and community similarity can be weak for bacteria perhaps indicating their most efficient dispersal across the drainage systems. It should be noted that, depending on the molecular method used, the taxonomic resolution in general may be lower for bacteria than for phyto- and zooplankton, thus possibly decreasing the spatial structure observed in the data.

The finding that communities showed strongest relationships with environment among phytoplankton was not surprising. Phytoplankton may be expected to be more strongly related to water chemistry compared to zooplankton, for example, as phytoplankton occupy low trophic level, often being under relatively strict environmental or bottom-up control (Paszowski and Tonn 2000). Higher trophic levels, such as zooplankton that graze phytoplankton, may be more strongly regulated by food web interactions or top-down forces (McQueen et al. 1989). Nutrient supply is the dominant factor influencing the community composition of phytoplankton. Longmuir et al. (2007) documented that trophic status of the lake is the strongest determinant of phytoplankton community structure in lakes in British Columbia. In spite of strong correlation with the local environment, phytoplankton communities were also spatially structured, indicating their dispersal limitation across the drainage systems.

I also documented that zooplankton exhibited the strongest spatial patterns in the data. This concurs with the idea that body size is influential on spatial patterns in community similarity and we predicted that zooplankton should show the strongest correlation between community similarity and geographical distance among the planktonic groups. This indicates that the dispersal ability of zooplankton is perhaps lower than that of phytoplankton or bacteria due to larger body size. This is in line with a study conducted on wetland pond plankton in boreal region (Soininen et al. 2007*b*). Of the environmental variables, the community composition of zooplankton was affected by the variation in water colour and water temperature. The high importance of water colour concurs with Beisner et al. (2006) who documented that zooplankton community structure was driven by nutrient and carbon supply in Canadian lakes. In contrast, Arnott and Vanni (1993) and Soininen et al. (2007*b*) emphasized the importance of

water pH or conductivity on zooplankton assemblages. Nonetheless, phytoplankton and zooplankton largely respond to similar environmental factors.

Overall, the local environment seemed to influence the communities to a larger extent especially for phytoplankton. This is typical for large-scale data sets collected in freshwater ecosystems (see e.g. Beisner et al. 2006). Even though I measured the key environmental variables for planktonic taxa, such as nutrient and carbon supply, surface area, depth and electronic conductivity, I had to rely on static snapshots on communities and environment because of inclusion of high number of sampled lakes. Turnover of the communities is often fast in small aquatic ecosystems thus resulting in a relatively small proportion of variation that could be explained using single sampling only. This unknown residual variation among the lakes is likely induced, for example, by spatial population dynamics among the lakes (i.e., stochastic extinction-colonisation events) and biotic interactions within the lakes such as predation by fish.

4.3. Scale-dependency in alpha and beta diversity

In this thesis, I also studied the scale-dependency in aquatic communities using boreal lakes as a study system. First, I found that alpha diversity in plankton communities showed scale-dependency. At local scale, plankton diversity and ecosystem productivity showed variable relationships, but at regional scale, two out of three relationships were positive linear. Second, I studied if beta diversity showed scale-dependency. I found that distance decay in composition was evident only at large, across-drainage system scale and that zooplankton showed strongest spatial distance decay among the planktonic groups. To sum up, spatial scale has a central role for alpha and beta diversity as results were weaker at small spatial scale in both studies (I-II). The reason for this may be that at small spatial scales, dispersal is efficient and environmental gradients are short, resulting in stochastic patterns. If the scale increases, both dispersal limitation and environmental gradients increase, thus leading to clear differences in species richness and composition (II).

4.4. Factors affecting temporal turnover in aquatic systems

I showed that beta diversity in time is strongly related to several ecological, physical and geographical variables (III-IV). For example, ecosystems showed differing rates of turnover as communities in oceans did not turn over as fast as freshwater ecosystems in seasonal data sets. It also appeared that turnover can be faster in tropics for studies covering short time spans, but the pattern can be reversed if long-term data are used. Moreover, organism body size was positively correlated with the slope, i.e., large organisms had slower long-term temporal turnover than the small organisms (paper III). Finally, it emerged that in boreal diatom communities, eutrophic streams did not show a greater degree of beta diversity in time than oligotrophic streams, probably due to counteraction by the stream size (paper IV, more on ecosystem size in section 4.5.).

There are multiple underlying drivers for temporal community variation. It is important to acknowledge that different ecosystem types, such as lakes, streams or seas can have variable rates of turnover in time and space. Clarke (1992) suggested that spatial beta diversity in marine ecosystems is weaker than in freshwater ecosystems. However, in this thesis I showed that physicochemically stable and geographically vast oceans can show temporal turnover as fast as freshwater ecosystems in interannual data sets. These results strongly agree with the studies on spatial turnover (Soininen et al. 2007a)

Besides varying across ecosystems, temporal turnover can exhibit large-scale geographical variation. Soininen et al. (2007a) documented strikingly similar scale-dependency in the latitudinal gradient of spatial turnover as was shown here in temporal turnover, i.e. turnover was faster in tropics at short time scales, but the pattern reversed at larger temporal scales. Faster turnover in tropics at short time scales probably results from higher energy input in low latitudes. Energy input affects the rate of life cycles, which is, in turn, directly linked to generation times and longevity (Brown et al. 2004). In addition, low latitudes are typically characterized by higher species diversity, which may have a destabilizing effect on population stability (Tilman et al. 2006).

Second, the finding that turnover is faster at high latitudes at long timescales concurs, for example, with Evans et al. (2007) who found that birds at low latitudes have slower temporal turnover compared with their northern counterparts. White et al. (2006) also suggested that the more species rich assemblages in tropics, for example, have slower rate of temporal turnover due to low environmental heterogeneity. In fact, it may well be that year to year variation is overall large in a seasonal environment (Berg & Bengtsson 2007).

Put together, the latitudinal gradient in temporal turnover can be scale-dependent: turnover is faster in tropics at short time scales but slower at long time scales. The mechanisms behind this remain speculative at present, but these outcomes may result because of the interplay between energy input and temporal variation in environment.

4.5. Temporal turnover and ecosystem size

Besides affected by several drivers mentioned in section 4.4., ecosystem size can also affect temporal turnover. In this thesis, I found that in some cases temporal turnover can be faster in larger ecosystems (III) and that ecosystem size can counteract with other factors affecting temporal turnover, such as organism size (III) and trophic state (IV).

Traditionally viewed, temporal turnover should slow down with increasing geographical extent as suggested by the general species-time-area relationship (Adler et al. 2005). However, temporal turnover can be faster in large ecosystems due to multiple reasons. Faster turnover in larger ecosystems may at least partly result from the counteraction between ecosystem size and organism size. This can be the case in paper III, where the major part of the stream data sets that represented the smallest ecosystems consisted of fish and zoobenthos that tend to turn over relatively slowly (see section 4.4.). Thus, factors affecting

temporal turnover can act in different directions, resulting in contradictory (III) or overall weak patterns (IV) in temporal turnover. Environment in general may play a crucial role in affecting the turnover rates and much of the unexplained variation in turnover can most plausibly be related to unknown temporal variation in environmental features. In fact, the lack of data on environmental heterogeneity through time represents a possible caveat for studies on temporal turnover, as species' occurrences are arguably affected by the fluctuating environmental conditions.

4.6. Implications for biomonitoring and biodiversity conservation

Large-scale studies combining both temporal and spatial community variation are urgently needed as global biodiversity diminishes at an accelerated pace. It is seminal to understand the underlying mechanisms of the factors affecting species richness and composition both locally and regionally in several types of aquatic ecosystems. However, as biomonitoring is usually conducted at relatively small scales only using a single organism group, such multi-scale and multi-taxon studies are urgently needed. This thesis shows that both spatial and temporal community patterns may vary widely among different aquatic groups or between ecosystem types. Thus, it is important to study further how different types of communities and ecosystems change and are able to adapt to changing environmental conditions, such as increasing water temperatures due to global climate change. I further highlight that community patterns are typically scale-dependent and ecological signals in the data (i.e. community variation along gradients) may be weaker at smaller scales than at larger scales. The finding of a faster temporal turnover
among small taxa suggests that biomonitoring using small taxa would probably need more frequent sampling than biomonitoring using larger taxa. The factors affecting spatial and temporal components of diversity have an effect not only on the distribution and the number of the organisms on Earth, but on socio-economic well-being of humankind as we benefit from many resources and processes that are supplied by natural ecosystems, i.e. ecosystem services.

4.7. Conclusions

In this thesis, I found that the relationships between ecosystem productivity and alpha diversity in plankton communities are highly variable, thus suggesting that productivity-diversity relationships may be context dependent in lakes. I also found scale-dependency in alpha and beta diversity highlighting that community patterns are typically weaker along environmental gradients at smaller scales.

Besides studying the spatial variation of communities, I showed that aquatic beta diversity in time is highly related to several ecological, physical and geographical variables such as organism body size, latitude or temporal duration of the studies. Ecosystem size seems to be one of the most significant factors affecting temporal turnover. In other words, temporal variation in communities has multiple underlying drivers. I encourage aquatic ecologists to study

the underlying drivers behind temporal and spatial variation in communities further in order to increase the understanding about how large-scale environmental changes may affect biological communities in the future.

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